

OBSERVATIONS ON LESSONIA.

CONWAY MACMILLAN.

(WITH PLATES XIX-XXI)

THE observations recorded in this paper have been made upon a plant cast up upon the beach of Vancouver island at Baird point, on the strait of Juan de Fuca. It was collected by Miss Josephine E. Tilden, August 3, 1898, and portions of it were distributed in her *American Algæ* under the name of *Lessonia littoralis* Farlow & Setchell, this determination having been made by Professor De Alton Saunders and kindly furnished us by him. The plant when collected was apparently quite fresh, and must have been developed near the point where it was found. The day before its collection, I am informed by Miss Tilden that heavy seas had been coming in, and these no doubt dislodged the plant and carried it up upon the beach. From the shape of the holdfast it must have been growing in a cup-shaped depression of the rocks from which it had been detached without great difficulty.

The general habit and appearance of the specimen is shown in *plate XIX*, taken from a photograph made under my direction by Mr. C. J. Hibbard, of Minneapolis. The plant was removed from its tank of formalose and spread out upon a table top, which was then tilted at an angle of 50° , and the camera was lifted close to the ceiling of the room, and depressed so that the view is not appreciably foreshortened and gives a fair idea of the plant. From the holdfast to the tips of the longest laminae this specimen measured two meters in length. At the base the holdfast measures 9^{cm} in diameter. Immediately above the holdfast area the stipe is irregularly branched, developing seven principal trunks, each of which soon branches again. Owing to its probable confinement in an almost hemispherical depression, the holdfast is extremely condensed and contorted. Viewed from

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below it presents in places an almost smooth fixation area, rounded off and mottled by the superposition of and compression together of the different hapteric branches. This generally bulbous base is irregular on one side, where a protruding corner of rock had entered it, and is hollow, indicating that many of the hapteric branches were turned under the base of the stem.

The main stipe can scarcely be distinguished from the holdfast by which its lower portion has been overgrown. Of the seven branches which arise the largest is 3.5^{cm} in diameter, while the smallest is 6^{mm}. All of these appear to be about the same age, and all are strongly fenestrate near the base. This, I presume, may be due to the growth of epiphytic animals and vegetation. The whole base of the plant is covered with a growth of bryozoans, together with *Cladophora*, *Rhodymenia*, and other algæ, while barnacles and sertularian hydroid colonies are growing in the lacunae. It is to the growth of some of these organisms that I am inclined to attribute the lattice-like and hollow character of the stipe area near the base. Similar pathological perforations and lacunae are found on distal regions, but not so abundantly. For the most part the more distal portions of the stipe are solid, as in the tribe *Lessoniæ* generally. Toward the base the stipe is cylindrical, but it becomes flattened distally. Thus, 20^{cm} above the holdfast, cylindrical branches 12^{mm} in diameter are developed. Along the same branch system 10^{cm} distally, the stipe is 12^{mm} by 8^{mm} in transection. Distally 8^{cm} of this, on the same branch system, the flattening is stronger, and sections 15^{mm} by 4^{mm} are found, while the terminal portions of the stipe which give rise to the separate laminae may be but 2 or 3^{mm} in thickness and 20^{mm} in breadth. The branching throughout is dichotomous, and the paired laminae are ordinarily produced in groups of four at the tips of the flattened stipe. Each lamina has what may be called a petiolate base, and this is sometimes cylindrical in cross section, though more often flattened. The general color of the stipe and holdfast is brown, and with slight change the tint persists beyond the petioles of the laminae. The laminae themselves are lighter in tint, becoming quite green

in the formalose preparation, but not so different in color in the fresh material.

The laminae, of which over eight hundred are present upon the specimen under observation, vary in length from 10^{cm} on weaker lateral branches to over a meter on the stronger and central branches. They are all ribbon-shaped, thin, and gradually attenuated to a point. Robust and well-developed laminae measure from 5–6^{cm} across near the base, but many of them are scarcely 1^{cm} in diameter. Some of the leaves have very well-marked midribs, while others are quite devoid of them, and it is the narrow leaves which are provided most constantly with midribs, while the broader leaves commonly do not develop them. Through the dichotomy of the plant it generally happens that two pairs of leaves are borne close together; that is the laminae appear in groups of four, of which two may be described as inner and the other two as outer. All four of the leaves may be of the slender type with midribs, or the two outer leaves may be broad and the two inner narrow. So far as this specimen shows, it is only upon the broad leaves without midribs that sori of sporangia are produced. When the midrib is present it is often very wide, reaching within 2^{mm} of the leaf-margin, but in many of the slenderer leaves the midrib is only one third the diameter of the whole lamina. There is a difference, too, between the broad and narrow leaves in their bases, the broad ones being often rounded, while the narrow ones are attenuate. Sori, when present, form patches 10^{cm} or more in length on both sides of the broad-based sporophylls. Two or three such sori are found in succession upon larger sporangium-bearing laminae, and give a somewhat blistered appearance to the leaf, owing to the characteristic loosening of the cuticle common to all Laminariaceæ.

The presence of two kinds of leaves has been already noted in other members of the genus, and the explanation given in some instances has been that the leaves are biennial. During the first year they fail to produce sporangia, but later, during the second year of their life, sporangia are produced upon them.

This is the explanation given by Areschoug¹ of the leaves of *Lessonia nigrescens* Bory. In *Lessonia fuscescens* Bory the older leaves are two-horned at the apex, this being caused by the carrying away of the upper part when decayed, as described by Hooker and Harvey.² In this species the sorus itself falls away from the frond and the old leaves must present a very different appearance from the younger ones. In *Lessonia littoralis* the larger leaves have lost their tips, but this does not seem to be due to a sloughing off of the sori, since the position of the latter is basal. The position of the two kinds of leaves in the species under consideration makes it somewhat difficult to believe that their difference is purely a matter of age. Unfortunately young material is not at hand, and this, as well as a large number of other interesting questions, must be held in abeyance. It is true that the sporophylls are more coriaceous than the slender sterile leaves, and as will appear in the histological portion of this paper the general structure of the sporophyll is nearly equivalent to that of the midrib in sterile leaves. Nevertheless, from the very constant position of the leaves upon the ultimate branches of the stipe, it is difficult to assign them different ages unless some modification of the ordinary development by basal splitting has arisen. Indeed some evidence of this may be derived from the specimen under observation, in which very often but a single lamina of the narrow form appears in the notch between two of the broad laminae, and in a few instances the single central lamina is split at the base, thus giving it two petioles. It is therefore possible to conceive how by the continued growth of the plant the pair of leaves of one year may be separated by the pair of the succeeding year. This again is very much as described for *Lessonia nigrescens* by Areschoug in the work cited, and it may be said also of *Lessonia littoralis* with tolerable certainty that there is a "true defoliation and a true foliation."

If all laminae at the end of a branch could be regarded as a

¹ARESCHOUG: Observ. Phyc. 5:8. 1884.

²HOOKE and HARVEY: Flora Antarctica 2:457. 1847.

unit and taken into the mind without reference to their different ages, a comparison might be instituted with such forms as *Alaria*, in which the sporophylls are lateral at the base of the main frond. In *Lessonia* the two middle younger laminae would represent the central portion of the generalized lamina, while the outer pair of sporophylls occupying a lateral position would represent the wings. Year after year, during the life of the plant, the process of basal splitting, exfoliation of the tip, and dichotomy of the stipe continues and there are constantly present groups of laminae typically in fours, the two inner representing the midrib portion (in which the basal split actually occurs), and the two outer essentially marginal areas of the hypothetical single lamina. Without developmental stages, comprising a series of young plants for comparison, it is scarcely possible to settle the points that have been raised.

The genus *Lessonia*, founded by Bory,³ has not a very large literature. The most entertaining account of the remarkable plants classed under this genus is that of Hooker and Harvey in the *Flora Antarctica* already cited. Here is pictured very vividly the habit of the antarctic forms as they appeared to the young Hooker upon his cruise as assistant-surgeon of H. M. S. *Erebus*, under command of Captain Sir James Clark Ross.

This and the following are truly wonderful Algæ, whether seen in the water or on the beach; for they are arborescent, dichotomously branched trees, with the branches pendulous and again divided into sprays, from which hang linear leaves 1-3 feet long. The trunks usually are about 5-10 feet long, as thick as the human thigh, rather contracted at the very base, and again diminishing upwards. The individual plants are attached in groups or solitary, but gregarious, like the pine or oak, extending over a considerable surface, so as to form a miniature forest, which is entirely submerged during high-water or even half-tide, but whose topmost branches project above the surface at the ebb. To sail in a boat over these groves on a calm day affords the naturalist a delightful recreation; for he may there witness, in the antarctic regions, and below the surface of the ocean, as busy a scene as is presented by the coral reefs of the tropics.

Hooker goes on to say how the massive stems of *Lessonia fuscescens* have been mistaken by ship-masters for driftwood, and

³ BORY: Duperry. Voy. Bot. Crypt. 1828.

how the Gauchos use the cartilaginous stem for knife-handles; at the same time he gives, especially for *Lessonia ovata*, an extremely useful and accurate discussion of the morphology, and does not fail to point out several important histological facts upon which, in general, later accounts have been based. The most extensive anatomical study in the genus with which I am familiar is that of Grabendörfer,⁴ whose results in a general way would apply to *Lessonia littoralis* as well as to the species of his investigation, *Lessonia ovata*. The figures given by him, five in number, illustrate but scantily the anatomical structure of the genus. I assume, also, that they were made from dried material, and the very different detail which I have found, and present in the accompanying plates, may be regarded as the result of studying material practically equivalent to fresh. The method of preserving large algæ in use at the University of Minnesota has not yet broken down in a single instance, although over a thousand jars of formalose material are on the shelves. Four per cent. solution of formalose is used, but after the first few months the jars are opened and fresh preservative substituted. After this it is our experience that disintegration does not occur.

Other literature which has been used in the study of this plant and has been more or less helpful is cited below.⁵

⁴GRABENDÖRFER: Beitr. zur Kenntniss der Tange. Bot. Zeit. 43:641. 1885.

⁵KJELLMAN: Laminariaceæ in Engler and Prantl Pflanzenfamilien I. 2:242. 1893.

WILLE: Ueber die Wanderung der anorganischen Nährstoffe bei den Laminariaceen. Festschrift für Schwendener. Berlin. 1899.

WILLE: Beitr. die Phys. Anat. die Laminariaceæ. Christiania. 1897.

ROSENTHAL: Zur Kenntniss von Macrocystis und Thalassiophyllum. Marburg. 1890.

WILLE: Bidrag til Algernes Physiologiske Anatomie. Stockholm. 1885.

RUPRECHT: Bemerkungen über den Bau und das Wachsthum einiger grossen Algen-Stämme. St. Petersburg. 1848.

RUPRECHT: Pflanzen aus dem nördlichen Theile des stillen Oceans. St. Petersburg. 1852.

REINKE: Beiträge zur Kenntniss der Tange. Pringsh. Jahrb. 10:371. 1876.

OLIVER: Sieve-tubes in Laminariaceæ. Ann. Bot. 1:95. 1887.

WILLE: Zur Anatomie von *Macrocystis luxurians*. Bot. Zeit. 42:801. 1884.

SETCHELL: On the classification and geographical distribution of the Laminariaceæ. Trans. Conn. Acad. 9:333. 1893.

MACMILLAN: Observations on Nereocystis. Bull. Torr. Bot. Club 26:273. 1899.

Histology.—The anatomical study of *Lessonia littoralis*, herewith presented, is based upon a series of slides made for me at my request by Mr. Harold L. Lyon, Instructor in the Botanical Department of the University of Minnesota. The material was all passed through the alcohols and embedded in paraffin in the usual way. The sections were cut upon a Minot precision microtome, and transferred gradually from clearing agents back to formalose water. Many of them were stained with aniline-water-safranin and aniline-blue, and permanent mounts in formalose water were prepared by sealing the cover slips at the edges. Mr. Lyon found that the ordinary mounting media distorted the sections, and after a few trials of other media he settled upon the formalose water as the best. I shall consider the different areas of the plant in order, beginning at the proximal regions.

The holdfast.—As has already been stated, the holdfast area of our specimen was much distorted and confused by the inextricable matting together and coalescence of originally separate branches. The primitive disk area was not definitely distinguished. Sections through the central and basal region of the holdfast showed a most confusing and irregular tissue, evidently the result of appression of hapteres to each other's surfaces. In cavities of the irregular mass of the holdfast some unattached hapteric branches were found, and these showed the ordinary dichotomous branching, cylindrial shape, and smooth green surface characteristic of the higher Laminariaceæ. They did not essentially differ in appearance from those of *Nereocystis*, described by me last year, nor from those of *Laminaria* previously described by Foslie and others. They measured less than 2^{mm} in diameter in ultimate branches, and forked repeatedly within narrow vertical limits. Cross sections showed them to be composed of a pretty homogeneous thin-walled prosenchymatous tissue in which the cells are of varying sizes, averaging from 6–30 μ in diameter. Towards the surface the diameter of the cells lying in the radius of the cylinder is elongated, and there is a general superficial cambial area extending around the

holdfast and continuous over its tip immediately under the epidermis. The epidermal cells and the layer underneath are the only ones that take a protoplasmic stain with avidity, but the layers within these, to the number of five or six, contain numerous sharply staining chlorophyll bodies. It is apparent, therefore, that the growth in thickness of the holdfast is essentially superficial, and its whole tissue is produced from the cambial areas somewhat as is phelloderm from the cork cambium of higher plants. The epidermal cells proper are much the smallest of all those that make up the holdfast area, averaging from $5-10\mu$ in height. There is no differentiated medullary area in the organ.

The longitudinal section of a haptere shows the customary structure, and serves to make clear that the growth in length takes place in the same way as does the growth in thickness. Toward the center of the section the cells are much elongated, running in some instances as high as one tenth of a millimeter in length. This length diminishes toward the tip of the organ, and directly under the tip a vertical section does not differ essentially in appearance from a transection. The dichotomous branching of the holdfast is due, as in *Nereocystis* and generally in *Laminariaceæ*, to the appearance of adjacent circular fields of cambium which undergo division more rapidly than the intervening and surrounding areas, so that the centers of these fields are protruded as the tips of the two new hapteric branches.

In older hapteres which have become matted together in the general holdfast mass, the walls are somewhat thickened in all the cells. Many of the cells are collapsed and distorted by pressure, and whole hapteric branches seem in places to be engulfed in the general tissue, reminding one of the appressions of hapteres to each other that often occur in other plants of the order. It does not seem probable that there is any rhythmical thickening of holdfasts or hapteres, such as takes place in the stipe of *Lessonia*, and produces the curious rings resembling those of an exogenous tree.

The stipe.—Very young stipe areas in *Lessonia* are much flattened, being morphologically nothing more than proximal areas of the lamina. As the plant grows, however, the region of the stipe undergoes a kind of secondary thickening, resulting in a ringed structure; and, by the greater thickness of the ring on one or both sides of the original flattened organ than over the edges, the whole stem changes from a flattened to a cylindrical body. The pith in all such cylindrical stems, even when they are very large, persists in its original thin and flattened structure, and does not appear in the form of cylindrical medulla as it does in *Nereocystis*. The pith is very often excentrically placed, and the number of rings of growth on one side may apparently be twice as many as on the other.

I have not found anywhere in the literature an adequate account of the anatomical basis of the phenomena which have been known and commented upon since the first discovery of *Lessoniæ*; and in the plates accompanying this paper an especial effort has been made to indicate the occasion for the ringed appearance so characteristic of the *Lessonia* stipe. It has long been suspected that the rings are in no sense annual rings, but it has been believed that they are connected with the development of the tufts of leaves in such a way that for each cycle of leaves there should be an additional ring of tissue developed in the older portions of the stipe. No doubt this view is correct, and from the exceedingly rapid growth of these gigantic algæ it is altogether reasonable to suppose that several rings might be produced in a single season.

Cross sections were made of a stipe 1^{cm} in diameter and nearly cylindrical in form. In this the pith was placed excentrically and measured 5^{mm} in length by 1^{mm} in breadth, and lay 2^{mm} from one side of the stem and 7^{mm} from the other. Five distinct rings of growth were apparent on one side of the pith, and but three upon the other. The pith itself looks almost precisely the same in vertical section as in cross section, and is made up of an anastomosing web of loosely interlaced filaments imbedded in gelatin and filled with reserve food materials. The pith does

not stop abruptly where the inner ring of cortical tissue abuts upon it, but occasional medullary filaments run out between the thicker walled and more compactly placed filaments of the cortex. Trumpet hyphæ, abundantly represented in younger pith, are not so conspicuous in material of this age. The characteristic sieve-tubes of *Nereocystis* and *Macrocystis*, as described by Parker, Wille, Oliver, and others, have not been seen in *Lessonia*. The tissue immediately outside of the pith has in cross-section much the look of sclerenchyma. The cells in longitudinal section are not conspicuously armed, nor, as one looks at the cross-section under the microscope, do they seem to lie in radial rows. The inner ring on both sides of the pith is principally composed of such cells as have been described. The transition to the next outer ring is more clearly marked in the gross structure than under the microscope, and at first I was much puzzled because the thin sections which showed the rings very conspicuously when held up to the light did not show them clearly when placed under an objective. The occasion for this seems to be that cells of the new growth are at first somewhat more armed, and in places stand in rows extending in a radial direction and at the same level. The walls, except over the ends of the arms, are very thick. This has been shown both in diagram and in camera-lucida sections in *figs. 8-16*. Cross sections taken through a region where the armed-cell tissue contains such radial rows at the same level will here and there cut eight or more cells in such a way that the whole row comes into view looking somewhat like a medullary ray. Since the different radial rows are not all cut through the central portions of the cells, most of the tissue will preserve its sclerenchymatous appearance and the "medullary rays," so-called (they are of course *not* pith rays), come out as streaks of lighter appearance in the cross section. As the new ring of growth grows older the cells shorten their arms and become more condensed in appearance. This shortening of the arms, together with a less parallel arrangement, makes the light streaks shorter, narrower, and finally indistinguishable from the structure around them in the

section. The difference then between the inner and outer face of a ring of growth lies in the more armed shape of the inner cells, and the less armed shape of the outer, and the optical characters of the more-armed cells in the tissue are rendered peculiar by their tendency to stand in radial rows for some distance at the same level. In general the outer rings show longer rays and a generally coarser structure than do the inner, while the innermost ring of all around the pith shows the rays but sparingly, and in cross section is almost everywhere strongly sclerenchymatous in aspect. In the outer zones I have seen as many as nineteen cells in one of the rays, showing that this number of armed cells stood at exactly the same level in a radial plane and were all cut directly through the middle when the section was taken. A comparison of the cross and long sections as presented in the plate should make this matter clear. None of the zones of growth, except the one immediately around the pith, are free over any considerable area from the rays resulting in the manner described. Lying outside of the outermost zone will be found the immediate products of the superficial cambium, not yet modified into the characteristic armed-cells, but presenting a more isodiametrical character. The actual cambial region seems to lie immediately under the epidermis. Throughout the cortical region and extending down to the region of armed sclerenchymatous cells chloroplastids are abundant, and the epidermal cells themselves, with the layers immediately beneath, take dense protoplasmic stains. There is probably division of cells going on in several of the layers under the epidermis, but it would seem to be more active close to the epidermis than in the deeper layers. Three or four layers of cells immediately under the epidermis are of the same prismatic shape as the epidermal cells proper, and almost as broad as high. Deeper cells become elongated in a direction perpendicular to the epidermis, and their walls become thinner. In vertical section they are seen to lie in definite rows. The distinction made by Grabendörfer between outer and inner cortex in *Lessonia ovata* seems to hold good also for *Lessonia littoralis*, but there is a gradual transition

from one area to the other, and the most abrupt demarcation is that between the inner cortex and the pith. Indeed cells which begin life as components of the outer cortex may later become modified into components of the inner cortex, as the stem thickens.

Some peculiarities of structure were noticed, especially globose thickenings where the arms of cells came together in the ray-like rows of inner cortex cells. These bodies of cell-wall substance in their position and form remind one quite exactly of similar structures common in Rhodophyceæ and recently figured for *Gigartina* by Miss Olson.⁶ The "Hohl-räume" of Grabendörfer I have not encountered in any of the sections under observation, but it is not improbable that they might exist in this species in older stipe areas. Granular cell contents are pretty abundant throughout the plant. The pith is particularly well supplied and the sclerenchymatous tissue of the inner cortex contains an abundance of granules.

In general it may be said of the older stipe of *Lessonia littoralis* that it consists of a strongly flattened pith surrounded by an inner cortex in which several zones of growth may be present, and an outer cortex consisting of a generally cambial group of cells arranged in from ten to twenty layers. Secondary thickening originates in the superficial cambial region, and the zonate appearance of a mature stem is due to the rhythmical production of more-armed and less-armed cells; but the difference between these is so slight that the optical distinction can scarcely be accounted for without taking into consideration also the peculiar juxtaposition of cells, especially in later zones, in radial rows at the same level.

Transition to the lamina.—The stipe becomes much flattened and the structure simplified in its distal portions. At the transition area, where the longitudinal rifts originate by which the laminae are separated from each other, the structure can be observed by sectioning the petiolate bases of laminae. These are sometimes nearly cylindrical, but generally more or less oval in cross section.

⁶Olson: Observations on *Gigartina*. Minn. Bot. Stud. 2: 154. 1899.

In this region the pith is large, composed of slender interlacing hyphæ, the majority of which seem to run transversely. Mingled with the ordinary hyphæ of the pith web are numerous trumpet hyphæ with the well-known sieve-plates, where the flared-out ends of the cells come in contact with each other. Very many of the trumpet hyphæ run transversely in the pith web, and they are perhaps rather less abundant in the perimedullary portion where they take principally a longitudinal direction. The interstices between the hyphæ are filled with gelatin, and immediately outside of the general mass of interlocking and interlacing filaments is a sheath of sclerenchyma, between the longitudinally extended cells of which occasional pith hyphæ extend transversely. The pith in this region occupies about one third of the diameter of the cross section. The remaining area is composed of three well-marked layers. Immediately outside of the pith is the narrow band of sclerenchyma just described, an area not staining deeply with aniline-water-safranin. Outside of this sclerenchyma lies a band of fundamental tissue having the appearance of parenchyma in cross section. The contents of the cells are not strongly granular. Outside of the last mentioned region is chlorenchymatous tissue, in which the cells show a marked tendency to develop with their long axes perpendicular to the epidermis. Surrounding the whole is a characteristic epidermal layer of low prismatic cells. The longitudinal section through this area does not show a development of the armed cells so abundant in older stipe and characteristic of the zones of secondary thickening, but the layer directly under the chlorenchyma is composed of almost isodiametrical cells rapidly changing in form to elongated-prosenchymatous in passing from the periphery towards the pith. The cells immediately around the pith are very long, some of them measuring 1^{mm} from end to end, while the lumen as revealed in cross sections is sometimes not over 2μ in diameter. This condition reminds one of the similar shaped sieve-tubes of *Nereocystis*, which occur in the corresponding region of young stipe and lamina, but no end plates or callus has been detected in these cells of *Lessonia*, which in other

respects resemble the true sieve-tubes in form. There seems to be the same evidence of passive elongation and occasional obliteration that was noted in *Nereocystis*, and the same fragmentation of nuclei no doubt initiates the process of elongation. Upon the comparison of *Lessonia* with *Nereocystis*, it would seem reasonable to describe the "true sieve-tubes" of Wille and Oliver as modified sclerenchymatous elements of the perimedullary cortex.

The splitting of the lamina has not been definitely studied in this material, but so far as can be judged from the observations that have been made it takes place in the same manner as previously described for *Nereocystis*.

The lamina.—The essential structural basis of the lamina and the arrangement of the tissues indicate its complete morphological equivalence to the stipe. The pith is of course greatly extended into a narrow ribbon, the cells of which while retaining the web structure are not conspicuous for granular contents, indicating that the stipe serves in some sense as a reserve organ, while the leaf, essentially photosynthetic, uses its pith more particularly as strengthening tissue and a conduction path. On each side of the ribbon-shaped pith parenchymatous tissue is developed outside of a narrow intervening layer of sclerenchyma. Underneath the epidermis chlorenchyma cells extend, in from five to ten layers. The epidermal cells are not so low as those of the stipe, but generally show a long diameter perpendicular to the surface of the lamina. A well marked cuticle staining deeply is uniformly present. The edges of the lamina are occupied by cells (belonging in part to the pith area and in part to the cortex) with small diameter and thick walls, and these give strength to the margin. In young leaves it is probable that the midrib area is not immediately differentiated. The appearance of a midrib is caused simply by the greater thickness of the cortex along the central portion of the lamina and its somewhat abrupt thinning out at the sides. I was unable to distinguish in the pith tract any distinction between that portion which lay in the midrib and the portions on either side, nor do the cortical

cells differ in character in midrib and wings. The midrib may therefore be described in *Lessonia* as a central longitudinal hypertrophic cortex-area of the lamina.

The structure and development of the sorus.—The development of the sorus in *Lessonia littoralis* does not differ in any important respects from that described by many observers for other genera of the Laminariaceæ. The epidermal cells elongate into paraphyses, from the bases of which the sporangia arise. The sporangia themselves in some instances become almost as long as the paraphyses, reaching a length of 45μ , but this is unusual. Commonly they are from one half to two thirds as long as the slender paraphysal filaments, and of an elongated ellipsoid or club-like form. The zoospores are about 4μ in diameter, and have been observed in different stages of formation. A peculiar condition which I have not seen in other Laminariaceæ exists in the exfoliated cuticle. This during the extension of the epidermal cells into paraphyses has become greatly thickened, and may separate eventually after the manner described long ago by Thuret.⁷ It does not always, however, in *Lessonia* separate as a continuous membrane, but is often broken up into pieces corresponding to the original epidermal cells and retaining a generally prismatic outline. Each paraphysis over a large area may carry on its end such a little cuticular cap.

The drawings of sections have been made by Miss Josephine E. Tilden, to whom I must express my thanks not only for this assistance, but for the specimen upon which my observations have been based.

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EXPLANATION OF PLATES XIX-XXI.

All sections not described as diagrammatic were drawn with a Zeiss camera lucida under a magnification of 600 diameters, and reduced one half in reproduction.

PLATE XIX.

Lessonia littoralis, from photograph.

⁷THURET: Ann. Sci. Nat. Bot. 1850.

PLATE XX.

FIG. 1. Diagram of end of branch bearing two pairs of leaves, the outer pair without midribs and bearing sori, the inner with midribs and without sori.

FIG. 2. Cross section of haptere showing epidermis, superficial cambium, and ground tissue.

FIG. 3. Longitudinal section of haptere through superficial area.

FIG. 4. Longitudinal section through central portion of haptere showing elongated parenchymatous cells.

FIG. 5. Section through older area of holdfast showing irregular and distorted structure due to appression and coalescence of original haptere branches.

FIG. 6. Diagram of cross section through stipe 12^{cm} above holdfast showing flat pith and zones of secondary thickening.

FIG. 7. Cross section through outer cortical area of stipe 1^{cm} in diameter showing epidermis, cambial tissue, chlorenchyma, and transition to sclerenchyma.

FIG. 8. Cross section through zone of secondary thickening showing portion of a "ray" caused by the section striking the middle of adjacent cells in a radial row; between two of the cells button-shaped masses of cell-wall substance have been developed.

FIG. 9. Section through same area as last showing two "rays" cut at slightly different levels so that the shapes of the component cells are different; the majority of the cells have been cut across their arms giving a sclerenchymatous appearance.

FIG. 10. Cross section through the zone of tissue nearest to the pith showing the absence of arms and consequently of "rays," and illustrating the general sclerenchymatous appearance of this region.

FIG. 11. Cross section through the pith of same stipe showing the anastomosing web of hyphæ with cells packed with reserve materials.

FIG. 12. Longitudinal section through outer cortex and epidermis; transition from armed to outer cells.

PLATE XXI.

FIG. 13. Longitudinal section through secondary growth zone of stipe illustrating the armed character of the cells and their arrangement side by side at the same level.

FIG. 14. Diagrammatic representation of the position maintained by the armed cells; cross sections at point *a* would show the ordinary sclerenchymatous structure, while those made at point *b* would show the "rays" as in fig. 9.

FIG. 15. Longitudinal section of stipe near the pith showing on the left hyphæ of the pith web, and on the right the sclerenchymatous cells of the inner growth zone.

FIG. 16. Diagram of cross and longitudinal sections through the petiole base of the lamina; *a*, outer cortex and chlorenchyma; *b*, parenchymatous tissue; *c*, sclerenchymatous layer around the pith; *d*, pith.

FIG. 17. Detail of cross section through same area as last, showing epidermal, chlorenchymatous, and parenchymatous tissue.

FIG. 18. Cross section same area as last and continuous with it, showing transition to perimedullary sclerenchyma with cells of the pith web running out from the central pith.

FIG. 19. Longitudinal section through the region of *fig. 17*.

FIG. 20. Longitudinal section through the region of *fig. 18*.

FIG. 21. Cross section of lamina through the wing.

FIG. 22. Section through a sorus showing sporangia with paraphyses, the latter capped by cuticular fragments corresponding to separate cells of the epidermis.